

ON THE TYPE SPECIES OF *MACROCEPHALITES*
ZITTEL 1884 AND THE TYPE SPECIMEN
OF *AMMONITES MACROCEPHALUS*
SCHLOTHEIM 1813

by J. H. CALLOMON

ABSTRACT. A precise interpretation of the familiar name *Ammonites macrocephalus* Schlotheim has been impossible up to now because the specimen regarded as type is lost and was known only through a poor figure in the pre-1758 literature. The Schlotheim collection however still contains two specimens which may have been syntypes. One of these is now designated neotype and described. It conforms with what has long been a widely accepted interpretation of the species and genus. This removes the necessity for a rather complicated nomenclatural argument embodied in an application by Arkell to the International Commission some twenty years ago to use its plenary powers to designate as type species of the genus *Macrocephalites* a species other than *Am. macrocephalus* Schlotheim, namely *M. verus* Buckman. This and some other related species are also discussed and described.

THE ammonites of the genus *Macrocephalites* must rank among the most familiar to geologists and palaeontologists the world over, yet the precise definition of the genus by its type species, and of the type species by its type specimen, have remained uncertain. Schlotheim's *Ammonites macrocephalus* was inadequately figured and barely described, but, being common in the classical region of southern Germany, specimens bearing the name were to be found in all the museums. Thus there grew up by tradition a widespread and generally accepted idea of the meaning of the name. Similarly, in the wave of generic splitting at the end of the last century, Zittel based the genus *Macrocephalites* on a group of some forty species, the 'Macrocephali' of von Buch; and the close natural relation of these to each other must have seemed to him so natural that he did not explicitly designate any one as the type species.

Modern refinements of technique have however made more precise definitions necessary particularly for stratigraphic purposes. The standard *Macrocephalus* Zone goes back to Opper (1857). As originally defined, it was a rather broad unit, roughly equivalent to the whole of our Lower Callovian today, and as late as 1905 Blake could write (p. 39): '. . . there is no doubt some advantage in speaking of "the zone of *Am. macrocephalus*", . . . but in this sense "the zone of *Macrocephalites*", using a generic term only, would serve the purpose equally well . . .'. This is no longer true. Using in part species of *Macrocephalites* as guide-fossils, the original *Macrocephalus* Zone of Opper has been repeatedly subdivided, and stratigraphical correlations at this refined level can be carried ever further afield, as far as, for example, Cutch and Madagascar. There remains a *Macrocephalus* Subzone of the *Macrocephalus* Zone (see Callomon 1964), as basal residue of Opper's original zone and hence as basal subzone of the Callovian Stage; and although definitions of the stratigraphical units are in terms of their contained faunal assemblages and not single species, the question arises whether indeed the zonal index occurs in the zonal type area at all. Conversely, if not, have beds previously ascribed to the same age at the type locality of the subzone (Somerset) and the

type area of the index (Swabia–Franconia) been mis-correlated? Alternatively, were ecological factors responsible for limiting the geographical distribution of the species? The prerequisite to any attempt at answering these questions is the most precise taxonomic definition of the species involved.

A solution to the taxonomic problem was proposed by Arkell (1951). He concluded:

(i) that Schlotheim's species *Am. macrocephalus* was uninterpretable in terms of the original type series (hereinafter referred to as 'Schlotheim specimens');

(ii) that the name, because of its familiarity and long use, should be preserved, and hence some subsequently chosen type specimen designated;

(iii) that, for various reasons, the specimen to be chosen should be the one in Opperl's collection figured by Zittel in his text-book (1885, first edition only, p. 470, fig. 655) under the name *Macrocephalites macrocephalus* ('Opperl-Zittel specimen');

(iv) that the shortcomings of Schlotheim's original descriptions notwithstanding, *M. macrocephalus* Zittel 1884 is a form recognizably different from *Ammonites macrocephalus* Schlotheim 1813;

(v) that realizing this, Buckman (1922, pl. 334A, B), refigured what he thought was Zittel's specimen under a new name *Macrocephalites verus* ('Opperl-Buckman specimen').

He therefore applied to the International Commission on Zoological Nomenclature to use its plenary powers:

(i) to designate the holotype by monotypy of *Macrocephalites verus* Buckman 1922 as the type specimen of *Macrocephalites macrocephalus* (Schlotheim 1813), of which *M. verus* thus becomes objective junior synonym;

(ii) to designate *M. verus* Buckman (= *M. macrocephalus* (Schlotheim emend)) as the type species of *Macrocephalites* Zittel 1884.

In anticipation of a favourable decision, he reproduced Buckman's figure of the Opperl-Buckman specimen of *verus* as type of *M. macrocephalus* both in the *Treatise* (Arkell 1957, fig. 351) and his *Jurassic Geology of the World* (Arkell 1956, pl. 37, fig. 6).

While taxonomically correct on the facts as then known, the application has not been proceeded with, for after the restoration of the collections in Munich following the dislocations of the last war it now appears that the Opperl-Buckman specimen is definitely lost. A decision by the ICZN along the lines of Arkell's application would therefore be abortive; there would still be no actual type specimen.

It is the purpose of this paper to put forward a solution based on new evidence, which falls fully within the compass of the Rules as they have been since 1960 (*International Code*, 1964) and requires no action by the Commission under its plenary powers. The new facts are twofold. Firstly, although Schlotheim's original definition of *Am. macrocephalus* referred only to a single specimen figured so inadequately by Baier in 1757 (text-fig. 1, this paper), it does not necessarily mean that this single specimen constitutes the sole member of the type series. There may have been further specimens in the author's collection to which he did not refer in print. Through the courtesy of Dr. Hermann Jaeger of the Humboldt University in Berlin, I have been able to borrow two specimens from the Schlotheim collection bearing Schlotheim's labels. They tally fully with his amplified description of 1820, and there is no evidence that they were not

already in his collection in 1813. They are therefore possibly syntypes. One of these specimens, which is well preserved and conforms both with Baier's figure, as far as this is possible, and with what has always been commonly understood under the name *macrocephalus*, will now be described and chosen as type. As it is not absolutely certain that it is a syntype and, even if it is, as there then exists a statement in the literature which can be construed as already designating Baier's (lost) figured specimen lectotype, it cannot unambiguously in turn be designated lectotype. Either way, however, it conforms to all the requirements of Art. 75 of the *Code*, and will be designated neotype.

Secondly, the lost Oppel-Buckman specimen, holotype of *M. verus*, is not the specimen figured by Zittel as had been supposed. The Oppel-Zittel specimen is distinct and not lost; it is also figured here.

THE TYPE SPECIES OF *MACROCEPHALITES* ZITTEL 1884

The genus was founded, originally as subgenus of *Stephanoceras* Waagen 1869, in the following way (Zittel 1884, p. 470):

Macrocephalites Sutner MS (*Macrocephali* p.p. of v. Buch, Quenstedt) (Fig. 655). Mostly large, involute shells rapidly gaining in size with broad rounded venter. Regularly ornamented at all stages with numerous sharp ribs which furcate once or repeatedly near the narrow and deep umbilicus. Peristome simple, crescent-shaped, without lappets or constrictions. Suture line deeply incised, 2-3 small auxiliaries at the umbilical seam. From the Brown Jura of Europe and the East Indies. Some 40 species. Examples: *A. Morrisi* Opp. (Bathonian), *A. macrocephalus* Schloth., *A. tumidus* Rein., *A. Herveyi* Sow., *A. Keppleri* Opp., *A. arenosus* Waagen, *A. elephantinus* Waagen (Callovian) etc.—Fig. 655: *Macrocephalites macrocephalus* Schloth. sp. Callovian, Ehningen (Württemberg).

In its original form the genus thus included at least forty species, of which seven were named. None was expressly selected as type: hence there is *no type by original designation* (*Code*, Art. 67(b), 68(a)).

Among revising authors, none between 1884 and 1910 discusses the question of the nominal type species of *Macrocephalites* explicitly. Blake (1905) does, however, point out that the specimen figured by Zittel differs significantly from that of Baier's figure—which he reproduced—and refers it to a new species, *M. typicus*. This has been the cause of subsequent confusion but is wholly immaterial: designation of a nominal type species is a matter quite independent of the correct identification or otherwise of a single specimen.

Lemoine (1910, p. 15) wrote: 'Ce genre a été crée en 1885 . . . Il correspond a l'ancienne section des Macrocephali; le géotype est *Macr. macrocephalus* Schloth.; . . .'. He was fully aware of the hitherto wide interpretation of the genus, being the first to draw up a comprehensive list of included species. So his statement constitutes an unambiguous *type selection by subsequent designation*.

Brief mention must also be made of Buckman (1922), who figured one of Oppel's specimens from Württemberg (the Oppel-Buckman specimen). In the legends to the two plates, he wrote:

Pl. 334A: 'MACROCEPHALITES MACROCEPHALUS; ZITTEL, 1884, Genotype Handb. Pal. I, p. 470, Fig. 655; "Ehningen (Württemberg)" Callovian Palaeont. Mus., Munich (Oppel coll.).
MACROCEPHALITES VERUS, NOV. Holotype'

Pl. 334B: 'AMMONITES MACROCEPHALUS, OPPEL 1857, Cit. Spec. Juraf. 547; (*Macrocephalites macrocephalus*; Zittel, genotype) "Ehningen; Basis der Kellowaygruppe," Limonitic stone
MACROCEPHALUS VERUS, NOV. Holotype'

Both plates are of the same specimen seen from different angles, and the two legends are the only evidence we have as to what Buckman had in mind in creating the new name *verus*. However, quite apart from the question whether the figured specimen is in fact the same as that figured by Zittel, and of the validity of defining a genus by a type specimen, the wordings constitute a deliberate attempt to select *M. macrocephalus* Zittel 1884 non Schlotheim 1813 in preference to *A. macrocephalus* Schlotheim 1813 as the type species of *Macrocephalites* despite at least Lemoine's quite explicit designation to the contrary, of which Buckman of course may not have been aware.

Spath (1928, p. 169) and Arkell sought to maintain this designation on the grounds that *M. macrocephalus* Zittel 1884 was interpretable in terms of type material whereas *A. macrocephalus* Schlotheim was not. This is no longer the case.

Conclusion. Genus *Macrocephalites* (Sutner MS.) Zittel 1884.

Type species. *Am. macrocephalus* Schlotheim 1813 by subsequent designation by Lemoine, 1910.

THE TYPE OF *AMMONITES MACROCEPHALUS* SCHLOTHEIM

The species was named by Schlotheim in 1813 (p. 70) as follows:

'*Ammon. macrocephalus* *Oryct. nor.* suppl. T. XII F. 8'

There was no further text of any kind.

In his second work of 1820 he gives a greatly amplified description (p. 70):

16. *Ammonites macrocephalus*. Aus der Gegend von Arau und dem Öttingischen in grössern und kleinern Exemplaren (12 Ex.)*

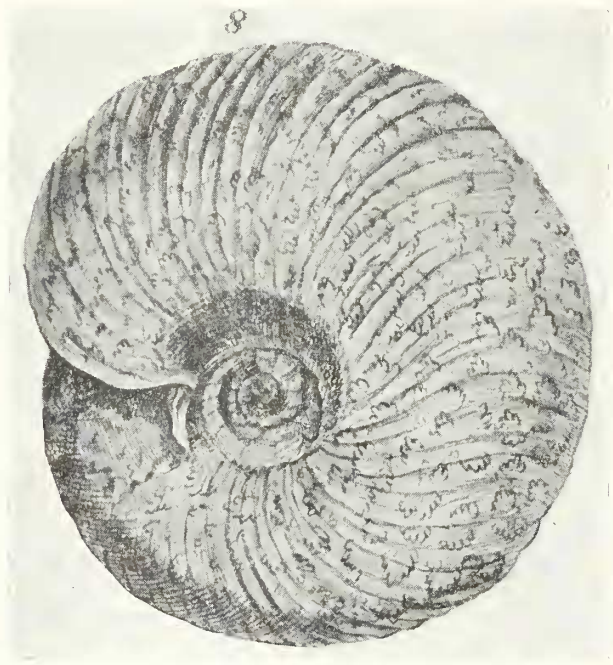
Ammonites Tumidus Reinecke T. V. F. 47

conf. *Oryctogr. Norica Suppl. T. XII. F. 8. Bourg. T 45 F. 286 variet.*

This is followed by an acceptable but general morphological description including some discussion of the variability of the species. Neither work is illustrated, and the only reference in 1813 to a figured specimen is to an old woodcut in a pre-1758 work by Baier (1757; text-fig. 1, this paper). As a result it is understandable that Blake (1905) in attempting to interpret the species should write (p. 43): '*Type*.—Schlotheim, having given no description of the species as distinct from the genus, and Baier, to whom he refers as above, having also left the shell nameless and without description, we are thrown back on the figure he gives as representing the shell called by Schlotheim *Am. macrocephalus*. . . This, therefore, must be taken as the type of *Macrocephalites macrocephalus*.' The last sentence can be interpreted as meaning either that Baier's figure was of the sole specimen, hence holotype, on which the species was based, or, if there were

* The copy of Schlotheim's book of 1820 in the British Museum states quite clearly '(2 Ex.)', although there is a gap in front of the '2'. Dr. Jaeger informs me that in the copy in the Humboldt University, on the contrary it states '(12 Ex.)'. The phrasing of the previous sentence 'in grössern und kleinern Exemplaren' supports the larger number, and the British Museum copy therefore presumably has a printing defect, in that the '1' of '12' did not register.

others not referred to, that it was thus designated lectotype. Either way, as Baier's specimen is lost, this is the origin of the view that Schlotheim's species is permanently uninterpretable unless a neotype of some sort is designated.



TEXT-FIG. 1. Photograph of figure from Baier (1757), quoted in Schlotheim's synonymy of 1813.

However, it is clear from the quotations given above that the difficulties attach only to Schlotheim's name of 1813: Blake's remarks do not apply to Schlotheim's work of 1820, in which he explicitly refers to twelve specimens from named localities in his own collection, and now includes Baier's figure only questionably in the species, prefixing it in the synonymy with 'conf.'.

Nomenclatorially there are three quite independent questions.

1. *Availability*. Schlotheim's name of 1813 appears to escape the non-status of a *nomen nudum* only through the reference to Baier's figure under Art. 16(a) (i) of the *Code*, and is therefore available in the sense of the *Code*. It has certainly always been regarded as such by subsequent authors, Blake included. Even if ruled unavailable in 1813 there would be no doubt about the availability of *Am. macrocephalus* Schlotheim 1820 instead, i.e. the question would resolve itself merely into one of the date of authorship. The only new problem this would create would be one of possible subjective junior synonymy with Reinecke's *Am. tumidus* of 1818. This is discussed further below.

2. *Type series*. Schlotheim's name of 1813 being available, the type series on which it is based includes *all* the specimens the author stated as belonging to the species (*Code*,

Art. 72(b)), including for instance, besides any referred to in print, any others in his own collection so labelled but not necessarily mentioned in the original publication. So even although the name owes its availability solely to the reference to the figure of Baier, Blake could not have been justified in assuming that Baier's specimen must be the holotype of the species without verifying that there were no additional specimens.

In fact the evidence indicates that there were. In 1820 Schlotheim himself referred to twelve. In a catalogue of his collection published after his death (Anon., Gotha 1832) and based on labelled specimens the number had fallen to 11. There is no direct evidence of the number in 1813, but we may not assume that it was necessarily less than two. The catalogue makes it clear in the introduction that Schlotheim was an avid collector rather than systematist, so that it seems highly unlikely that he would have founded a new species on specimens of which he had none in his collection. The type series of 1813 consisted therefore most probably of at least two specimens (Baier's being one).

3. *Type designation.* Blake's reference to Baier's specimen as the type of Schlotheim's species appears to have been on the presumption that it was the only specimen and hence holotype. Alternatively, it can be interpreted as lectotype designation. In either case the specimen is lost, and even if syntypes (paralectotypes) are subsequently found they can never displace its previously established role as type specimen. Such syntypes, or indeed as may be the case here, any other specimens in the collection of the original author subsequently identified by him as belonging to the species, are obvious candidates for the selection of a neotype, to replace the original type, provided they are satisfactory in all other respects. These are (i) that the neotype shall conform closely with the published descriptions and figures of the lost type; (ii) that it shall be typical, i.e. belong to the species as currently interpreted and not be a variant of the original species which has been split off and is now generally classified under a different name; (iii) that it shall have come from as nearly as possible the same locality and horizon as the previous type specimen. Of these, (i) and (iii) present no great constraint in the present case, for little is known about the origin of Baier's specimen other than that it probably came from Franconia, in the region of Nürnberg. One of the surviving specimens in Schlotheim's collection fills the prescription on all counts and is chosen as neotype and described below.

SYSTEMATIC DESCRIPTIONS

Macrocephalites macrocephalus (Schlotheim 1813)

Plates 15, 16

Ammon. macrocephalus Schlotheim 1813, p. 70.

Ammonites macrocephalus Schlotheim 1820, p. 70.

Macrocephalites leei Spath 1928, p. 169.

Selection of neotype. The Schlotheim collection arrived at the Humboldt University in Berlin in 1833 and was catalogued in the subsequent four years by Quenstedt who was then custodian (1888, p. 1102). The catalogue still exists and indicates that there were then more than 35 specimens of *Ammon. macrocephalus* in the collection. Dr. Hermann

Jaeger has kindly searched the collections of the Humboldt University and writes as follows:

Our *Macrocephalites* collection suffered strongly from rain water after the war. Many labels have been washed out and are no longer readable. Therefore it appears hard to tell how many specimens were those of Schlotheim's. I could detect only two. One is a beautiful big steinkern [A] with Schlotheim's label attached, on which only the words '*Ammonites macrocephalus*' can be deciphered. This specimen has been labelled *Macrocephalites tumidus* by a later worker. Schlotheim's label of the other specimen [B] runs as follows: '*Ammonites macrocephalus*, varietas *comprimata* (B). Aus Jurakalk der Gegend von Arau, Schweiz'.

Both Schlotheim's work of 1820 and the Gotha catalogue of 1832 refer to specimens from Arau, the latter to only one, so there seems no doubt that of these two surviving specimens one [B] was already in Schlotheim's collection in 1820. The other specimen [A] appears to be the only one to have carried one of the characteristic orange labels actually attached to it, which is still there. The Gotha catalogue refers to the disorganized state into which the collection had fallen because of the pressure of other work which prevented Schlotheim from devoting as much time to it as he wished. It seems a safe conclusion therefore that this only other properly labelled specimen was also one of the earliest in the collection. Finally, there is no reason to believe that they were not already in the collection in 1813. All the evidence therefore indicates that they may well have been members of the original type series of Schlotheim's species.

The larger of the two syntypes [A] is a magnificent macroconch phragmacone belonging to the genus *Macrocephalites* s.s. as interpreted by all subsequent authors. It is here designated neotype. The other specimen, [B], from Arau, is a poorly preserved microconch phragmacone 70 mm in diameter with the body chamber partly preserved, belonging to the subgenus *Dolikephalites* or *Kamptokephalites*. It resembles closely *M. (K.) lamellosus* Jeannet 1955, pl. xxvi, fig. 3, from bed A5 at Herznach near Arau (Enodatum Subzone of the Calloviense Zone), and is in similar matrix.

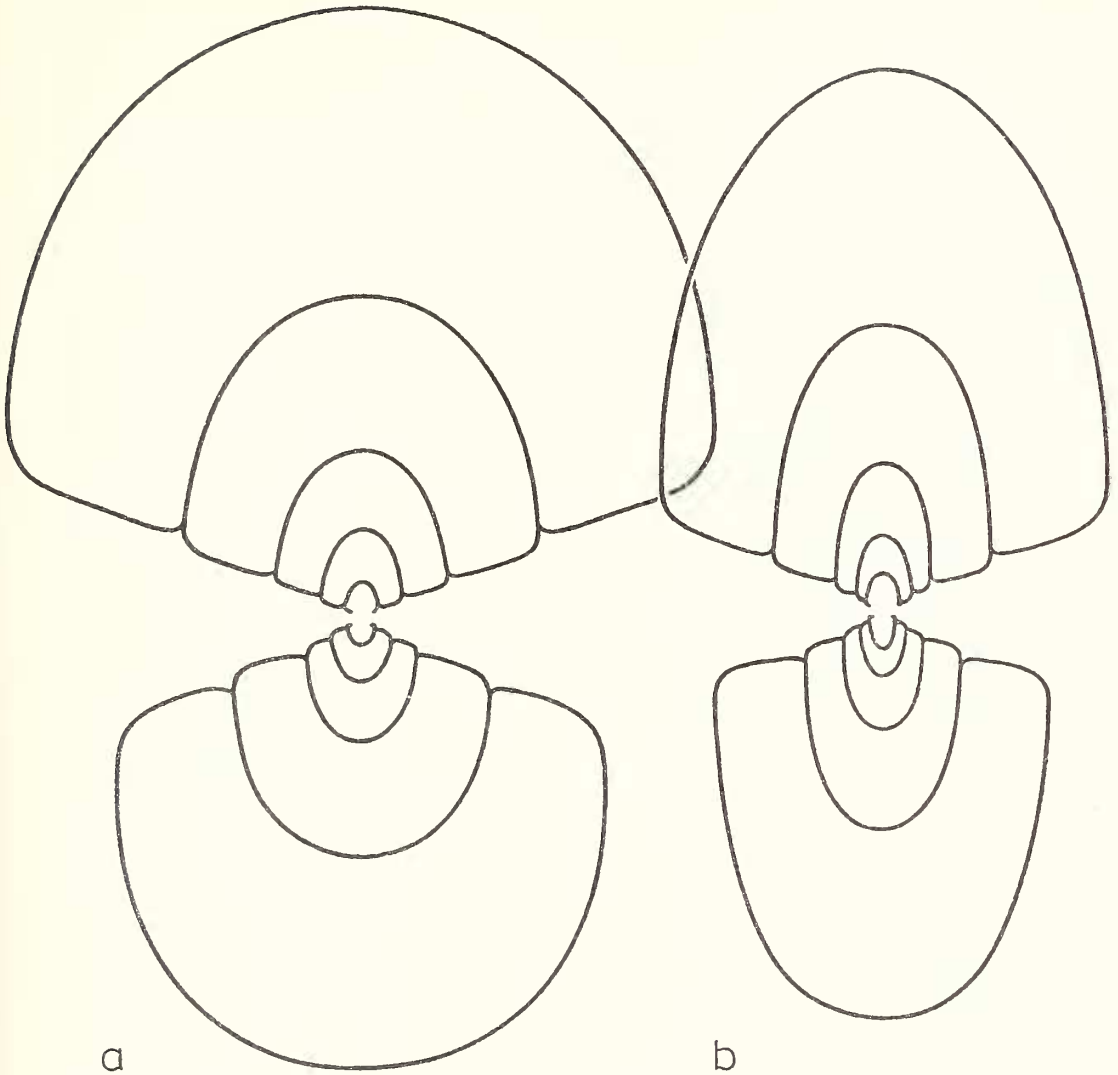
A plaster cast of the neotype is deposited in the British Museum.

Description of the neotype. A wholly septate cast, maximum diameter 140 mm, with no appreciable degeneration or approximation of the last septal sutures which do however merge into each other.

Proportions:

<i>Am. macrocephalus</i> Schlotheim neotype	<i>M. verus</i> Buckman holotype (Opper-Buckman specimen)	<i>M. macrocephalus</i> Zittel 1884 (Opper-Zittel specimen)
At 140 mm: 51, 67, 16 110 mm: 51, 68, 16	90 mm: 54, 55, 14	127 mm: 53, 49, 13
Secondary ribs: c. 120	c. 115	c. 125

The ribbing is dense and fine. The primary ribs are faint where the last whorl emerges and die out altogether soon after, at a diameter of 100 mm. They are faint even on the umbilical walls of the inner whorls, on which they rise and then pass over to the whorl-sides with little forward twist. The ribs furcate indistinctly very low on the whorl-side into secondaries which pass with pronounced forward sweep over the broad rounded



TEXT-FIG. 2. (a) Cross-section of neotype of *Macrocephalites macrocephalus* (Schlotheim 1813), figured in Plates 15 and 16. (b) Cross-section of *Macrocephalites macrocephalus* Zittel 1884 (non Schlotheim) figured in Plates 17 and 18, fig. 1.

venter where they are strongest, persisting feebly to the end of the preserved shell. The umbilical walls are steep, the umbilical margins moderately rounded. The whorl-section is shown in text-fig. 2a; the outer whorl was traced directly from the shell, the inner whorls from the parts exposed in the umbilicus together with a logarithmic spiral half-whorl constant (the ratio of spiral diameters at angles $(\theta + \pi)$ and θ) of 1.38. The septal sutures are elaborate and deeply incised as is typical of the genus, but not well enough visible to be worth figuring.

Schlotheim's orange label reads, under ultra-violet light, ' . . . *macrocephalus* Sch. . . othm/*Am. tumidus* Reinecke', and the specimen still bears the Quenstedt catalogue number in ink 'A 26'.

Origin of the neotype. Schlotheim refers to his specimens as from 'dem Öttingischen'. Dr. Arnold Zeiss informs me that this means the land that belonged in former times to the Dukes of Öttingen, a small town at the northern end of the Ries, 15 km NE. of Nordlingen, 60 km SW. of Nürnberg, i.e. at the southernmost end of the Franconian Alb. Geological maps show that the Brown Jura is here not prominent but does occur in greatly reduced thickness in scattered outliers capped by small patches of White Jura (Gerstlauer 1940). Dorn (1939, p. 165) has described a section at Heidenheim, 12 km NE. of Öttingen, and ascribes some 1.25 m of yellow to brown more or less oolitic marls to the *Macrocephalus* Zone. He records *Macrocephalites macrocephalus* Schlotheim from it here and elsewhere, the nature of the beds changing little over considerable distances: von Ammon's description (1875, p. 41) of them in the region of Regensburg is almost identical. Gerstlauer (1940, pp. 31–33) records *M. macrocephalus* from several places in similar beds in the more immediate vicinity of Öttingen itself.

The neotype is preserved in a yellow marly limestone. The adhering matrix is a yellow marl with small shining brown ooliths. The lithology thus agrees perfectly with that described in the literature from Franconia, including Öttingen, and matches that of other specimens from the region in the museums.

Comparable material. There are few figures in the literature that resemble the neotype at all closely. The region that has produced most comparable material appears to be Swabia, and with the exception of a few specimens figured by Quenstedt, the fauna has never been properly described. Two specimens in the British Museum are very close to the neotype: BM no. C.1139, from 'Hornberg, near Gmünd, Württemberg'; and BM no. 22361 from 'Lochen', Württemberg. The latter is one of the syntypes of *Macrocephalites leei* Spath (1928, p. 169), and is here designated lectotype. The other syntype is *Amm. macrocephalus rotundus* Quenstedt 1886, pl. 76, fig. 11, from Achdorf. As Spath correctly pointed out, these forms are not to be confused with *M. tumidus* (Reinecke), discussed again below, just because they are inflated. *M. leei* Spath is therefore a direct subjective synonym of *M. macrocephalus* (Schlotheim).

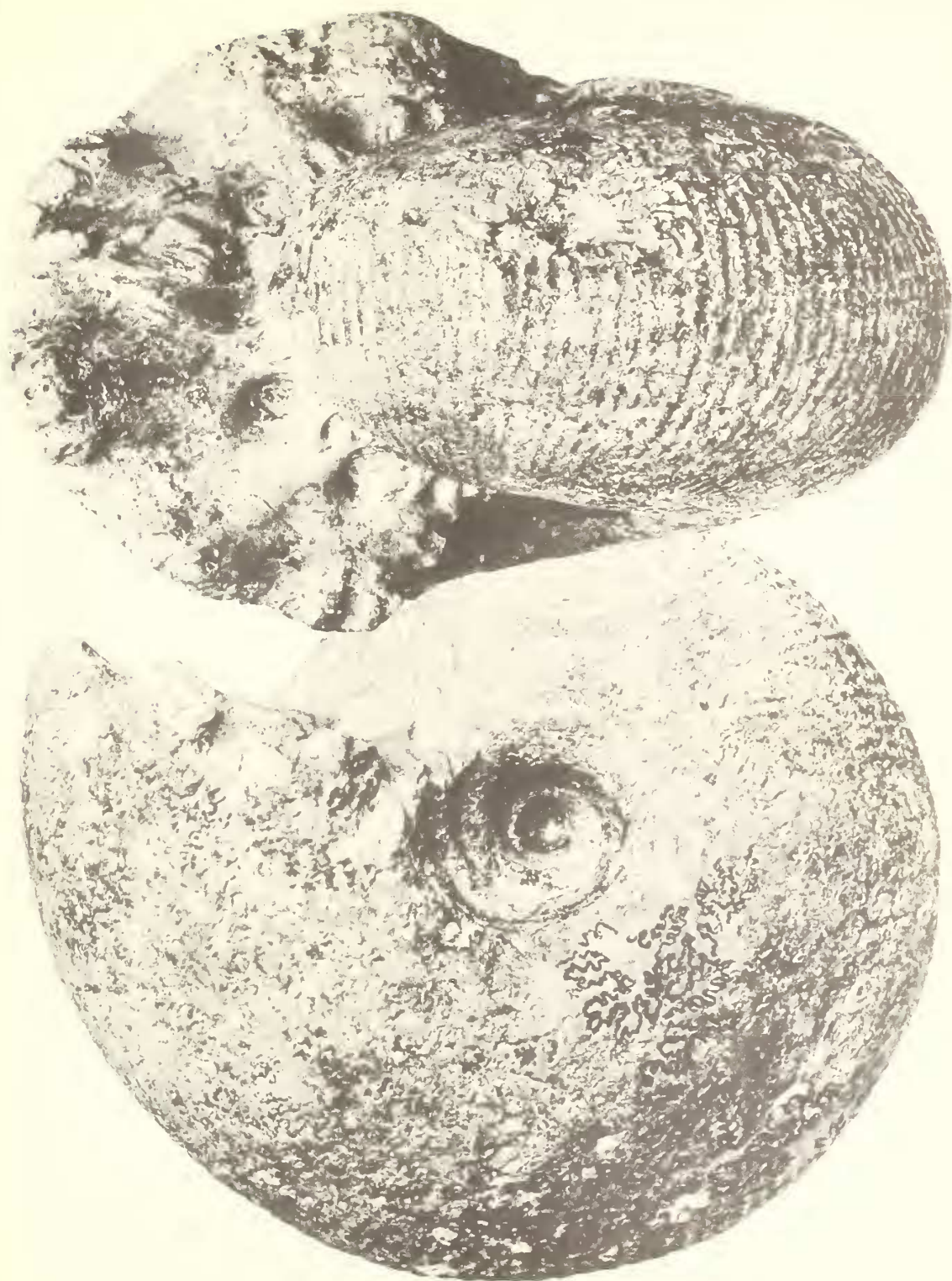
Forms like the neotype of *macrocephalus* appear to be extremely rare in Britain. Large well-preserved macroconchs are in any case not numerous in the collections, and it is difficult to say to what extent collection failure is the cause. The closest match is perhaps an old specimen in the British Museum (BM no. 32607), lacking details of origin, preserved in the matrix of a concretion from the lower Kellaways Clay of Dorset or Wiltshire. It bears attached *Exogyra nana*, and came therefore probably from

EXPLANATION OF PLATE 15

Macrocephalites macrocephalus (Schlotheim 1813), neotype. Side and front views, natural size. Schlotheim collection, Humboldt University, Berlin.

EXPLANATION OF PLATE 16

Macrocephalites macrocephalus (Schlotheim 1813), neotype. Rear view, and side view lit differently from that in Plate 15.



CALLOMON, *Macrocephalites*



CALLOMON, *Macrocephalites*

the Kamptus Subzone of the Macrocephalus Zone. The Upper Cornbrash has produced a number of very large, inflated *Macrocephalites* s.s. from the neighbourhood of Malmesbury, Wiltshire, while having the general form and style of ribbing of the Franco-Swabian group to which Schlotheim's specimen belongs, they seem yet consistently slightly different, in being bigger and more strongly ribbed. One in the Institute of Geological Sciences is very close. It is septate to 180 mm, with a little body chamber, and has the following dimensions:

IGS no. FJ 11: at 145 mm: 50, 75, 13; c. 100 secondary ribs.

It is from Charlton, Wilts., bed 4 (Douglas and Arkell 1928, p. 136). Like most of the specimens from this area, it came from a high part of the Macrocephalus Subzone of the Macrocephalus Zone (transition from *siddingtonensis* to *lagenalis* brachiopod zones).

Comparison with other forms and variability of the species. It was in part Arkell's submission in trying to establish *Macrocephalites verus* as the type species of *Macrocephalites* that, influenced largely by Zittel's choice of figure, popular interpretation of the name *macrocephalus* had veered away from the inflated forms exemplified by Baier's figure to more compressed forms, the inflated ones being called *M. tumidus* (Reinecke); and that any attempt now to revert to the original concept would upset well-established and widespread usage. In this view Arkell was closely following Spath (1928, p. 168).

There is no doubt that the compressed forms such as shown in Zittel's figure (and including *M. verus*) are common, occur widely, and have been often described. Yet, curiously, a perusal of the literature shows that these common forms were rarely called *M. macrocephalus*, but usually described instead under a long list of other names; whereas to judge by the hesitation, at least in modern times, with which the name itself has been used, the species itself seems to be everywhere rare. The literature of the last sixty years, i.e. since attempts to refine the taxonomy beyond the comprehensive species of *macrocephalus* and *tumidus* began, in fact reveals no well established and widespread usage.

The truth of the matter appears to be that inflation of the shell is in *Macrocephalites*, as in other sphericonic ammonite genera, not a closely defined biospecific character; and in an adequate sample of a population there are seen to occur all intermediate stages between the most inflated and the most compressed. This view was already clearly stated by Spath himself (1928, p. 19). The diagnostic features of the group of *M. macrocephalus* (Schlotheim) are the fine, dense ribbing; early fading of the primary ribs to give smooth whorl-sides; involute coiling with narrow steep-sided umbilicus and sharp umbilical edge; and sub-triangular to semicircular whorl-section with maximum width at the umbilical edge. It seems probable therefore that, assuming them all to be of the same age, *M. macrocephalus* (Schlotheim)—*M. verus* Buckman—*M. macrocephalus* Zittel 1884 non Schlotheim are simply variants of a single biospecies ranging in thickness from at least 49% to 68% of the diameter (see proportions given above). Even this probably does not cover the full range. Not all the variants occur with equal frequency and the commonest seem to be the more compressed. If this view were correct, the taxonomic consequences would be simply to reunite all the forms under the venerable Schlotheim name. In the present state of knowledge however such 'lumping' would create more problems than it would solve—the current dilemma in so much of ammonite

systematics—for then everything depends on being able to recognize a true sample of a homogeneous, strictly contemporaneous population. Yet in the present case most of the literature describes relatively small samples of varying and largely unknown relative ages from widely separated localities. Morphologically precise and usable descriptions of individuals are a prerequisite for the identification of populations and thus bio-species, and to this end separate Linnaean specific names for morphologically distinguishable forms typologically defined will have to continue to be used pending more extensive stratigraphic and monographic studies. No attempt is therefore made here to set up more extensive synonymies of Schlotheim's species, and a separate description of Zittel's species is given below.

Macrocephalites tumidus (Reinecke), to which were referred many forms in the past simply because they were inflated, belongs to a distinct group which is stratigraphically younger. It is also briefly discussed further below.

Age of the neotype. The 'Macrocephalen-Oolith' or oolites of southern Germany are notoriously condensed, often in a marly phosphatized remanié facies. Even if the exact provenance of the neotype were known, it seems unlikely that its precise age in terms of standard subzones could have been established there, for there are up to now no independent guide-fossils in the basal Callovian other than the brachiopods used in the Cornbrash in England. All that one can hope to establish in Swabia or Franconia is local faunal associations, and then to recognize the same assemblages in vertical succession in expanded sequences elsewhere.

All the forms described above, which are from the region between Balingen and Öttingen, do give the impression of forming a single characteristic assemblage. Associated with it is *Kepplerites keppleri* (Oppel) (including *Ammonites macrocephalus evolutus* Quenstedt) common around Ehningen, found in England in thin basal Upper Cornbrash at Long Handborough near Oxford (Douglas and Arkell, 1928, pp. 128–9, bed 4; Callomon 1959, p. 511; Oxford University Museum, 5 specimens). This is in the *siddingtonensis* brachiopod zone, i.e. *Macrocephalus* Subzone of the *Macrocephalus* Zone, but as the bed is thin it is impossible to be more precise. It has unfortunately here yielded no macrocephalites. Quenstedt figures other forms of *Macrocephalites* which are almost certainly younger than the *macrocephalus* assemblage, e.g. the original of his *Anm. macrocephalus rotundus* (1849, pl. 15, fig. 2) from Achdorf on the Wutach, near Blumberg, south Baden. The 'Macrocephalen-Oolith' in this area is more like that at Herznach, Aargau, than in Württemberg and belongs to the upper Calloviense Zone. As noted above, the second syntype of *M. leei* Spath also came from this locality and may thus equally be younger than the neotype of *macrocephalus*. It was because of this uncertainty that it was here not chosen as lectotype of Spath's species.

In England, where the detailed stratigraphy of the Lower Callovian is well known, the nearest forms to Schlotheim's from well-localized horizons came from the upper part of the *siddingtonensis* brachiopod zone near Malmesbury where it is thicker than usual, i.e. from a level definitely some distance above the base. Even these forms, however, are not quite the same as those from southern Germany. Beds younger than those of Malmesbury have produced abundant faunas at many levels and these are all quite distinct.

To summarize, therefore, the exact stratigraphical horizon of *M. macrocephalus*

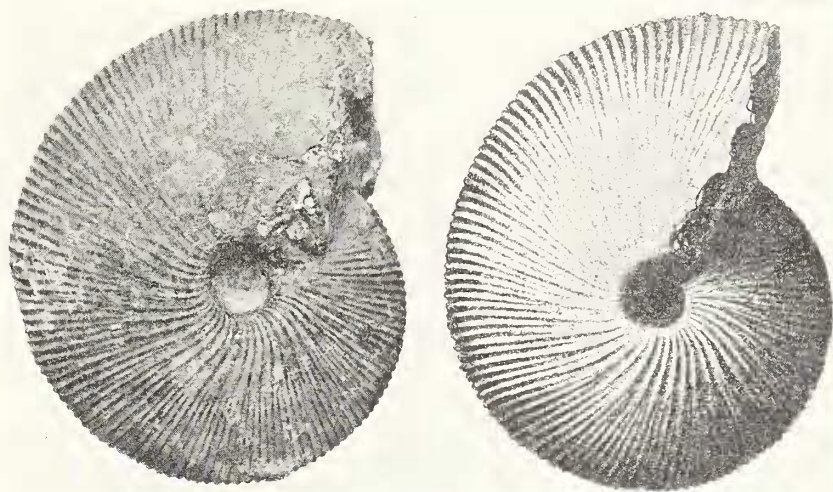
(Schlotheim) remains to be determined. Uncondensed sequences rich in ammonites appear to be uncommon in the classical areas of Europe, although to judge from a brief visit in 1969 the succession at Cap Mondego in Portugal may provide a valuable exception. The species as exemplified by the neotype has not so far been found in the type-area of the *Macrocephalus* Zone in England, but indirect evidence indicates strongly that (a) this is due to collection failure; (b) that the species does occur in the standard Zone and Subzone of which it is the index; and (c) that its position therein is in the lowest part.

Macrocephalites macrocephalus Zittel 1884 non Schlotheim

Plates 17, 18, fig. 1, text-figs. 2b, 3

Macrocephalites macrocephalus Zittel 1884, p. 470, fig. 655.

Identification of the specimen. The legends to Buckman's plates of *M. verus* are ambiguous. It seems clear that he intended to designate Zittel's specimen as 'genotype'



TEXT-FIG. 3. Reproduction of Zittel's figure (1884, fig. 655), and a photograph of the specimen reduced $\times 0.5$.

of *Macrocephalites*, i.e. in effect as type specimen of the type species, two things that he rarely, if ever, regarded as distinct; but then, if he regarded the specimen he figured as being the same as that figured by Zittel, as Spath and Arkell assumed, why should he have renamed it '*Macrocephalites verus*, holotype'? It seems much more likely that he did so knowing it to be *not* the specimen figured by Zittel.

The type of *verus* is lost, but Zittel's specimen still exists. Through the courtesy of Dr. Werner Barthel I have been able to borrow it. Accompanying it is a label in Buckman's handwriting with the words 'Zittel's Genotype'. Zittel's original figure is reproduced here in text-fig. 3, together with a photograph reduced $\times 0.5$; and except for some exaggeration of the rate of growth of the spiral it can be seen to give quite a good

impression of the shell. The specimen is in the Staatssammlung für Paläontologie, Munich, reg. no. AS VIII 119. A cast is deposited in the British Museum.

Description. The proportions were given above (p. 120) with those of Schlotheim's neotype. The whorl-section is shown in text-fig. 2*b*, the inner whorls being drawn with a spiral half-whorl constant of 1.37.

The specimen is a wholly septate macroconch of diameter 127 mm. The test is largely preserved and septal sutures are invisible. The section is sub-triangular with rounded venter and maximum thickness near the umbilicus. The umbilicus is deep and narrow with steep walls and well-defined margin. The ribbing is fine, sharp, and dense, the primaries rising slightly rursiradiately up the umbilical wall, sweeping with pronounced forward twist over the umbilical margin, and then bi- or trifurcating irregularly and inconspicuously by intercalation and passing almost straight up the whorl-sides. The primaries, *c.* 45 to the whorl, fade and finally disappear at 120 mm to give an almost smooth whorl-side, the secondaries persisting on the venter. There is nothing to indicate the former extent of the shell, but the absence of any signs of further septa suggests that only the body-chamber is missing.

Locality and horizon. The specimen came from the Macrocephalen-Oolith of Ehningen, Württemberg, as did the types of *M. verus* and *Kepplerites keppleri*. Unless the bed is there condensed, which is not improbable, this suggests basal Macrocephalus Zone. For discussion, see above under neotype of Schlotheim's species.

This form does occur in England. The specimen figured by Arkell (1933, pl. xxxv, fig. 1, 1*a*; Oxford University Museum no. J20437) is slightly fatter than Zittel's, but otherwise very similar in all respects. It is septate to 145 mm, and the umbilical suture extends to another $\frac{2}{3}$ whorl with strong uncoiling. It came from Shorncliffe, Glos., between Malmesbury and Cirencester, out of the lowest part of the Upper Cornbrash, lower *siddingtonensis* zone (Douglas and Arkell 1928, p. 135, beds 2-3). Another specimen in the Institute of Geological Sciences (IGS no. 25632) is almost indistinguishable. Its origin is unrecorded, but the preservation is typically that of Upper Cornbrash of southern England.

Synonymy. The list of figures resembling Zittel's is very long, but the following are some of the names that have been used in the Indo-European realm.

- (a) *Ammonites formosus* J. de C. Sowerby 1840, pl. xxiii, fig. 7; holotype refigured by Spath, 1928, pl. xxiii, fig. 1*a, b* (Cutch, India).
- (b) *Ammonites macrocephalus compressus* Quenstedt 1849, p. 184, pl. 15, fig. 1 (Swabia).
- (c) *Stephanoceras Cannizzaro* Gemmellaro 1870, p. 45, pl. ix, figs. 9-11 (Sicily).
- (d) *Ammonites Jacquoti* H. Douvillé 1878, p. 570 (= nom. nov. for (b)).
- (e) *Macrocephalites compressus* Blake 1905, p. 45 (= (b)).
- (f) *Macrocephalites madagascariensis* Lemoine 1911, p. 51; 1910, pl. v, fig. 3*a, b* (Madagascar).

EXPLANATION OF PLATE 17

Macrocephalites macrocephalus Zittel 1884 (non Schlotheim), natural size. Opper collection, Munich, no. AS VIII 119, from Ehningen, Württemberg.

EXPLANATION OF PLATE 18

Fig. 1. *Macrocephalites macrocephalus* Zittel 1884 (non Schlotheim). Same specimen as in Plate 17, obverse side.

Figs. 2-3: *Macrocephalites tumidus* (Reinecke 1818), topotypes.

Fig. 2. BM. no. C29337. Fig. 3. BM. no. C29336. Both specimens from Uetzing, Bavaria, Model collection. All figures natural size.